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Allomaternal care, life history and brain size evolution in mammals

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Abstract

Humans stand out among the apes by having both an extremely large brain and a relatively high reproductive output, which has been proposed to be a consequence of cooperative breeding. Here, we test for general correlates of allomaternal care in a broad sample of 445 mammal species, by examining life-history traits, brain size, and different helping behaviors, such as provisioning, carrying, huddling or protecting the offspring and the mother. As predicted from an energetic-cost perspective, a positive correlation between brain size and the amount of help by non-mothers is found among mammalian clades as a whole and within most groups, especially carnivores, with the notable exception of primates. In the latter group, the presence of energy subsidies during breeding instead resulted in increased fertility, up to the extreme of twinning in callitrichids, as well as a more altricial state at birth. In conclusion, humans exhibit a combination of the pattern found in provisioning carnivores, and the enhanced fertility shown by cooperatively breeding primates. Our comparative results provide support for the notion that cooperative breeding allowed early humans to sidestep the generally existing trade-off between brain size and reproductive output, and suggest an alternative explanation to the controversial “obstetrical dilemma”-argument for the relatively altricial state of human neonates at birth.

Keywords: allomaternal care, brain size evolution, cooperative breeding, life history, mammals

Introduction

Humans are characterized by a high level of allomaternal care (e.g. Hrdy 2009), which has been proposed as the original catalyst for many later steps in hominization (Burkart et al. 2009; Hrdy 2005; see also Aiello and Wells 2002). The cooperative breeding hypothesis (Hrdy 2009) claims that psychological characteristics such as proactive prosocial (or other-regarding) preferences arose as a result of cooperative breeding, since they are also found in cooperatively breeding callitrichids (Burkart and van Schaik 2010). We have also argued that cooperative breeding in early hominins, through energy subsidies for mothers and weaned children, may have allowed for the steep increase in encephalization (Isler and van Schaik 2009a; Navarrete et al. 2011), without a concurrent reduction of the rate of reproduction. This claim warrants substantiation.

Here, we use a broad comparative approach to test predictions concerning the effect of allomaternal care on brain size derived from an energetic framework (Isler and van Schaik 2009a), which argues that the growth and maintenance of brain tissue (Mink et al. 1981) usurp a considerable proportion of an animal's energy budget. Because reproduction is also energetically expensive (e.g. McNab 2006; Speakman 2008; Zenuto et al. 2002), Isler & van Schaik (2009a) argued that one major pathway toward the evolution of larger brains was reduced allocation to growth and reproduction ("production" in Charnov 1993). Indeed, among altricial mammals, increased brain size (always assuming constant body mass) is correlated with reduced litter size, whereas among precocial mammals, mostly producing singletons, it is instead correlated with reduced birth rate (Isler and van Schaik 2009a). The young of relatively large-brained precocial species develop more slowly and attain sexual maturity at a later age than young of relatively small-brained species. Moreover, all larger-brained mammals

produce relatively larger neonates, which may buffer against the serious long-term effects of starvation or malnutrition on brain development and functioning (for humans, e.g. Kar et al. 2008; reviewed in Levitsky and Strupp 1995). Not surprisingly, therefore, we also found that relatively large-brained mammals have reduced annual fertility. All these effects of brain size add up to produce a strong negative correlation between brain size and maximum possible population growth rate (r_{max}; Isler & van Schaik 2009b). Because of this tradeoff between brain size and reproductive output, the basic prediction is that the evolution of allomaternal care in a lineage facilitates an evolutionary increase in either brain size, by allowing greater energy allocation to the brain, fertility, or both (albeit each to a lesser extent), in comparison to its independently breeding relatives.

Allomaternal inputs (henceforth "help") are found in many eutherian mammals, comprising behaviors such as provisioning, carrying, huddling or communal nesting, babysitting, and protection from predators or defense of resources against conspecifics. This help is therefore a mix of (direct or indirect) energetic inputs and general protection. Its effects on offspring survival or fertility have been demonstrated within species (reviewed e.g. in Silk 2007; Snowdon 1996), and also between carnivore species (Gittleman and Oftedal 1987; Moehlman and Hofer 1997). One likely mechanism underlying this effect is load-lightening of lactating females by helpers, which has been demonstrated e.g. for meerkats (*Suricata suricatta*) (Scantlebury et al. 2002) and for primates, in which fathers and older siblings carry their offspring (callitrichids: Bales et al. 2000; Garber and Leigh 1997), siamangs: (Lappan 2009). In communal breeders, other adult, usually reproducing females provide the help through babysitting or allonursing (Packer et al. 1992). This support may reduce peak maternal loads (König 2006) and load-lighten mothers also on average, if the provided care is

non-depreciable, i.e. that the costs of huddling or babysitting do not increase with the number of offspring (Clutton-Brock 1991). In sum, there is ample empirical evidence that distributing the costs of reproduction over several (or at least two) individuals yields an energetic benefit for mothers.

Previous studies of the relation between allomaternal care and brain size have reported mixed results. Gittleman (1994) found that independently breeding carnivore mothers have relatively larger brains than communal or biparental breeders. On the other hand, species in those carnivore families that are characterized by frequent occurrence of helping behaviors (Canidae, Herpestidae, and Hyaenidae) formed an exception to the rule that larger-brained mammals have lower fertility (Isler and van Schaik 2009a). For primates, Ross (2003) quantified allomaternal care according to percentage of time spent with conspecifics other than the mother, and found a negative correlation between the amount of allomaternal care and brain size. In marsupial mammals, species that exhibit allomaternal care have relatively larger brains than solitary species or species that live gregariously without showing allomaternal care (Isler 2011). In corvid birds, cooperative breeders are not relatively larger-brained than pair-breeding species (Iwaniuk and Arnold 2004). Most of these studies, however, relied on a categorical distinction between species with and without help, whereas from an energetic perspective the actual amount of allomaternal care may be more important.

The aim of this paper is therefore to quantitatively examine the effect of various helping behaviors on fertility and relative brain size in eutherian mammals as a whole as well as in various speciose radiations within this taxon. We do not expect this prediction to differ between precocial and altricial mammals, because help is not only effective during the period of brain growth (i.e. mainly during gestation in precocials and during lactation in altricials, cf. Dobbing and Sands 1979), but also during the period when the

offspring's brains are much larger relative to body mass than in adults, and thus proportionally much more expensive (i.e. during lactation in precocials). Thus, we expect that the energetic effects of allomaternal care allow mothers to increase fertility or relative brain size in both altricials and precocials (prediction 1). Beyond this general prediction, we also predict that the strength of the effect decreases from those helping behaviors that provide a direct energetic benefit, such as provisioning, to more indirect benefits that reduce the mother's burden such as carrying, huddling, or babysitting, to potential benefits such as protection (prediction 2).

However, the amount of help may also affect the developmental stage at birth. On one hand, a shift towards more altricial offspring would increase the effectiveness of help, by resulting in a reduced load for the mothers during gestation. Thus, in a bird species, the superb fairy-wren (*Malurus cyaneus*), mothers laid smaller eggs in the presence of helpers, and subsequently exhibit increased survival rates (Russell et al. 2007). For mammals, only those precocial taxa that are able to shelter their offspring from predation, such as primates, should be able to afford such a shift towards more altricial offspring (prediction 3). On the other hand, if help mainly increases the survival rate of offspring, a quality-over-quantity strategy should be more successful and we predict a shift towards fewer, but more precocial offspring (prediction 4).

We test these predictions using a large sample of 445 eutherian mammal species, for which there is reliable information on brain and body mass, as well as the nature and extent of allomaternal help. We first investigate the clustering of the different helping behaviors, and their distribution among various mammalian clades. We subsequently analyze the effect of these components of help on both brain size and life-history variables, while controlling for the effects of phylogenetic relatedness and several potential covariates. In particular, since a positive correlation between brain size

and allomaternal care could also arise from a social effect (the “social brain hypothesis”, e.g. Dunbar 2009), and because cooperative care requires a social lifestyle, we include *gregariousness* as a covariate in all analyses to disentangle the potential effects of social settings and allomaternal care.

Methods

Data

The full dataset is available as an Electronnic Appendix. Taxonomy follows Groves (2005) for primates and Wilson and Reader (2005) for all other mammals. Data on brain and body mass as well as life history parameters of eutherian mammals were compiled from various sources (the compilation is described in detail in Isler and van Schaik 2009a). If available, we used sex-specific values, preferring female to male values. If sex-specific values for brain size were not available for a species, but sexual dimorphism in body mass is reportedly pronounced (more than 10% difference), we used the body mass of the smaller sex, usually female, to reduce error variation.

Values on allomaternal care behavior and ecological variables were compiled from published compilations (Bronson 1989; Dewsbury 1985; Emlen 1991; Gittleman 1994; Gubernick and Klopfer 1981; Hayes 2000; König 1997; Packer et al. 1992; Ross and MacLarnon 2000; Silk 2007; Snowdon 1996; Solomon and French 1997; Spencer-Booth 1970; Whitten 1987; Wilson and Mittermeier 2009; Woodroffe and Vincent 1994), the Mammalian Species accounts (1969-2009), reliable online sources (Animal Diversity Web, Myers et al. 2006) and original sources for individual species (for a full list of references, see Appendix).

In total, data on helping behavior and brain size were available for 445 species of eutherian mammals. Chiroptera and Cetacea were excluded from being sampled because reliable data on allomaternal care and life history characteristics of both cetaceans and bats are notoriously difficult to obtain (see Supplementary Information for a discussion). Eusocial bathyergid rodents were not included as it was not clear from published records of brain size and body mass data (Mace et al. 1981) whether the size dimorphism between reproductive and non-reproductive adults was adequately considered.

Helping behavior

We need a measure of help that reflects energetic inputs to the mother or her offspring. For our purposes, it does not matter here whether helping behavior is costly for the donor, whether the help is depreciable (Clutton-Brock 1991) or not, or whether there is reproductive skew or not. However, it may well matter what kind of help is provided: carrying, provisioning, allonursing, thermoregulation, protection from predators, or defense of feeding range (the latter two may indirectly improve maternal energy budgets). Thus, helping behavior was divided into the following categories: carrying, provisioning, allonursing, thermoregulation/babysitting and protection. Carrying and provisioning, as the energetically most costly behaviors, were recorded separately for the father and other group members. We aimed at obtaining a quantitative measure of these helping behaviors by considering their frequency of occurrence (results using an alternative, categorical coding scheme are generally similar, see Appendix). If the published records of allomaternal help were vague regarding these frequencies, we put the emphasis on adequately reflecting the difference between closely related species in our values, as this difference is most relevant in a phylogenetic comparative approach.

Thus, the difference or similarity of a value between sister taxa is much more robust and reliable than the absolute values. Coding was done in order to yield variables between 0 and 1 as follows:

"Provisioning by the male": This refers to the frequency of provisioning by the male (usually, the breeding male in pair-living species, but, rarely, any adult male in polygynous or multi-male, multi-female groups). It was set to 1, if the male usually actively shared or provisioned food, to 0.75 if passive sharing was more frequent (70-80%) but active sharing was common (20-30%), to 0.5 if passive sharing was common and active sharing rare, to 0.1 if passive sharing was rare, and to 0.05 if single observations of food sharing or provisioning were reported.

"Provisioning by others": The frequency of provisioning or food sharing by other group members was assigned using the same scoring system as for the male.

"Carrying by the male": This refers to the frequency of carrying by the male. If the offspring was carried 50% of the time by the male, the value was 0.5. When carrying behavior was limited to pup retrieval it was counted in the category of Thermoregulation, etc. below.

"Carrying by others": The frequency of carrying by other group members was assigned using the same distinctions as for the male.

"Protection": This refers to the occurrence of active protection by the male, defense of territory, or defense against predators. It was considered absent if territories were only protected against other males, and females or young may even be hurt during agonistic encounters between males. Otherwise, we scored protection as 1 if it was usual, 0.5 if frequent, 0.1 if rare, and 0.05 if single observations were reported. If more precise values were given in the original sources, those were used.

"Thermoregulation, babysitting and pup retrieval": This refers to the occurrence of babysitting during mother's absence, retrieving pups, or carrying offspring to a new nest, by the male or other group members, huddling, and communal nesting (together with male or other females, breeding or non-breeding) during the breeding period. It was scored as follows: 1 if it was usual, 0.5 if frequent, 0.1 if rare, and 0.05 if single observations were reported. If more precise values were given in the original sources, those were used.

"Communal nursing" (allonursing): This refers to the frequency of allonursing of an infant. The values given by Packer et al. (1992) were converted as follows: "1" (<10%) was set to 0.1, "2" (10-45%, less than own mother) to 0.25, and "3" (as much as own mother) to 0.5. If more precise values were given in the original source, these were used.

If a behavior is only shown during part of the period of offspring dependence, the value was weighted accordingly (e.g. in *Symphalangus syndactylus*, the male is carrying the offspring 100% for one year out of a total of two; thus the value for male carrying was set to 0.5). Finally, if a species was described as solitary and territorial, or aggressive against conspecifics (often most pronouncedly during the breeding period), all help values were set to zero.

"Provisioning of mothers": This behavior was classified as 0: absent, or 1: occurring. Scoring was this crude because frequencies were not reported in the literature.

Covariates

In large-scale comparative analyses, the potential effects of hidden variables, which may cause spurious correlations between the variables of interest, is considered, if feasible, by including these variables as covariates in the analyses. For example,

living in social groups could be the underlying factor responsible for a positive correlation between brain size and allomaternal care, and we therefore included gregariousness as a covariate to control for this effect. Living in social groups ("gregariousness") was classified as follows: 0: solitary (or mother with infants), 0.5: usually solitary, but occasionally seen in pairs or groups, or facultative group denning, 1: pairs (with infants), 1.5: usually in pairs, but gregarious at times or in part of the range, 2: permanently gregarious (the group comprises more adults than just the parents).

Diet quality, activity pattern, and substrate use have also all been suggested to correlate with relative brain size (e.g. Harvey and Bennett 1983; Harvey et al. 1980; Harvey and Purvis 1999), in Primates (Fish and Lockwood 2003; Kirk 2006), Carnivora (Gittleman 1986), and Rodentia (Bernard and Nurton 1993), and although it is less clear how these variables could be related to allomaternal care or fertility, we also included them as covariates. Since we were not aiming to explain the ecological correlates of brain size evolution, but rather aimed to control for them, diet quality, nocturnality and substrate use were coded empirically in a way so as to explain as much of the variation in brain size as possible (see Supplementary Information).

Although some variables were found to have significant effect on brain size in some groups, on the whole, controlling for these variables did not affect the level of significance of the results for helping behavior. This can be attributed to the use of phylogenetic methods, which are known to reduce the influence of possible confounding variables as these are usually also similar between closely related taxa (Nunn and Barton 2001).

Analyses

As a data reduction technique to tease out patterns from sets of highly correlated variables, we applied principal components analyses (PCA) to the set of allomaternal care variables, using JMP 7 (Inc. 1989-2009). Varimax rotation was applied to those factors with Eigenvalues larger than 1. In comparative analyses, the problem of different degrees of relatedness between species must always be addressed (Felsenstein 1985). Therefore, we also ran a phylogenetic PCA (PPCA) using R code from Revell (2009) and the R package GPArotation (Bernaards and Jennrich 2005). As the Eigenvalues of the phylogenetic principal components were all very low, the phylogenetic PCA was not useful as a means of reducing the complexity of the data, but the results can still be used to investigate the robustness of our results from the species-level PCA. Therefore, the results of phylogenetic PCA are reported in the Appendix only.

All morphological and life-history variables were log-transformed before analysis. The correlations of the help factors with brain size or life history traits were analyzed with multiple linear regression models. To control for the effects of other variables known to exhibit correlations with brain size or life history traits in at least some taxa, *adult female body mass*, *diet*, *activity period*, *substrate use,* and *gregariousness* were included as covariates. To incorporate an empirical estimation of the degree of phylogenetic relatedness in the data, which is represented by the parameter lambda, phylogenetic general linear models (PGLS) are commonly applied (Nunn 2011). We used the caper package in R (Orme et al. 2011) to fit models that control for phylogenetic relatedness, estimating lambda by maximum likelihood. Phylogenetic relationships and molecular branch length estimations were taken from the species-level supertree of Bininda-Emonds et al. (2007), refined and supplemented by more recent molecular phylogenies as listed in the Supplementary material. However, to

illustrate our findings, species or suborder mean values and residuals from non-phylogenetic multiple least-squares regressions are shown in the figures.

All analyses were conducted on three levels: in the combined sample of placental mammals (N=445 species), within large orders of similar lifestyle (fissiped Carnivora (N=101), Rodentia (N=113), Primates (N=98), and Artiodactyla (N=66)), and on the level of suborders (N=28 suborder means). The latter provides a valuable alternative to investigate the contributions of small clades that are usually swamped by the larger clades in phylogenetic models. The effect of provisioning of mothers could be investigated only in Carnivora, as it is not reported in other nonhuman mammals.

Results

Prevalence of helping behaviors

Figure 1 illustrates the distribution of helping behaviors during breeding in eutherian mammals. Provisioning is most frequent in Carnivora and Primates and almost absent in other groups. Protection by the male, in the absence of any other help, is observed in about 20% of primates and artiodactyls. Allonursing without any other form of help is mainly found in artiodactyls and in pinniped carnivores. Overall, primates stand out in that some form of helping behavior is almost ubiquitous, whereas it occurs in less than half of the species in the other groups.

Components of help

To obtain a simplified and orthogonal set of variables representing allomaternal help, we ran a principal components analysis (PCA) on the components of help. The PCA yielded two principal components (Table 1a). The first factor is loading on all

helping behaviors except communal nursing, and is therefore referred to as “allocare”, whereas the second factor “allonursing” is loading mainly on communal nursing.

Within the major orders, the clustering of helping behaviors differs according to lifestyle (Table 1b). In Carnivora, the first factor loads most strongly on protection and provisioning by the male, but also on pup retrieval and babysitting, while provisioning by other group members groups with allonursing score high on the second factor. In Rodentia, the first factor loads on provisioning, whereas allonursing groups with communal nesting and protection score high on the second factor. In Primates, the first factor is dominated by provisioning, but comprises all allomaternal care behaviors except allonursing, which loads on the second factor. In Artiodactyla, allonursing and babysitting both load on the first factor, whereas the second factor represents protection by the male. In sum, the distinction between allonursing and the other helping behaviors is not as clear as in the combined mammalian sample, and we also need to analyze the large orders separately in order to investigate the effects of the components of helping behaviors on brain size and life history traits in detail.

Allomaternal care and brain size

In placental mammals as a group, the first principal component of help (cf. Table 1a) is positively correlated with brain size on the level of suborders, controlling for phylogenetic relationship, body mass, gregariousness, diet, nocturnality and substrate use (Table 2a, Figure 2). However, no significant correlation between help and brain size is found in a phylogenetic species-level analysis (Table 2b), because the relationships within some large orders exhibit opposite trends (Table 2c).

Relationships within the large orders are illustrated in Figure 3. In terrestrial Carnivora, both factors of help are significantly positively correlated with brain size

(Figure 3A, note that non-phylogenetic regression models do not show the positive effect of allonursing), while gregariousness shows a weak negative trend. In Rodentia (Figure 3B), the first factor, provisioning, is positively correlated to brain size and the second one, communal nesting and protection, shows a positive trend. A look at the results of the phylogenetic PCA reveals that in this order protection is positively correlated with brain size, whereas communal nesting/babysitting/pup retrieval is not (Appendix Table 3). Thus Figure 3B depicts the phylogenetic principal component "protection". In Primates (Figure 3C), allonursing is positively correlated with brain size, but other help such as provision and carrying is negatively correlated with brain size in the phylogenetic models. In Artiodactyla (Figure 3D), the first factor comprising allonursing and babysitting shows a very weak positive trend with brain size ($p=0.185$), and gregariousness also shows a positive trend.

In sum, allomaternal energy inputs are correlated with brain size in mammals overall (on the suborder level), and in three out of four large orders. Whereas the effect is mostly positive, the direction is opposite for "allocare" in primates. In all groups, the effect of direct help such as provisioning or carrying is stronger than that of indirect help such as babysitting, huddling, or protection.

Allomaternal care and fertility

In mammals as a group, on the level of suborders only the second principal component of help (cf. Table 1a) was positively correlated with fertility (Table 3a and b). Again, the phylogenetic linear regression models testing the effects of helping behavior on fertility include potentially confounding variables as covariates (body mass, gregariousness, diet, nocturnality and substrate use). On the species level, and within Primates (Table 3c), we find a positive effect of the first factor, "allocare", on fertility.

This positive effect is stronger than the simultaneous positive effect of gregariousness on fertility. In fissiped Carnivora, the second factor, “allonursing”, shows a positive trend with fertility. Overall, help is less frequently correlated with fertility than with brain size, and the two effects are complementary.

Allomaternal care, development and longevity

Analyses of other life-history traits are summarized in Table 4. In mammals as a group, on the suborder level there are no significant correlations. On the species level, the only significant correlation is found between allomaternal care (PC1) and maximum lifespan. Within orders, in Primates, allocare (PC1) is negatively correlated with gestation length and the length of the lactation period, whereas gestation length is positively correlated with provisioning (PC1) in Rodentia, and with protection (PC2) in Artiodactyla (again, as above, controlling for potentially confounding effects and phylogenetic relationships). Gregariousness is associated with a later weaning age in Carnivora, but an earlier one in Rodentia. The age at first reproduction is not related to helping behaviors in any group, but more gregarious species mature later in Artiodactyla. Maximum lifespan is positively correlated with allonursing (PC2) in Primates and shows a positive trend with PC1 in Rodentia. Overall, then, where help affects life history, it most commonly affects the earliest stage of development, gestation, suggesting that it modifies the lineage’s modal developmental state at birth (precociality or altriciality), but it does not do so in the same direction in each clade.

Provisioning of mothers

In Carnivora, we could also test for the effect of provisioning the mother in those species that provision their offspring. We found that provisioning of mothers is an

additional positive effect on brain size (Table 5), but does not affect the life-history variables.

Discussion

The mammalian pattern

Using a large compilation of frequency based measures of helping behavior during breeding in mammals, we found support for all predictions flowing from the energetic framework of brain size evolution. Our first prediction was that energy subsidies from non-mothers allow species to evolve larger brains relative to other species where mothers bear the burden of raising offspring alone (prediction 1). Controlling for body size and the effects of phylogenetic relatedness, as well as for some possibly confounding variables, our analyses supported this prediction. The effect of help on fertility, on the other hand, was complementary to the effect on brain size, and was found mainly in the order of Primates.

The amount of phylogenetic structure in the data was high (lambda values mostly close to 1), necessitating the application of phylogenetic methods. However, if trends within groups do not match the larger pattern found between clades, due to grade shifts which result from differences in lifestyle, phylogenetic models yield different results than analyses of species-level data (e.g. the effect of allonursing on brain size in Carnivora is significantly positive for PGLS, but not for raw species analyses). In this case, results of phylogenetic analyses are more reliable.

In some of our analyses, however, trends within different clades were completely opposite, as in the relationship between allocare (PC1) and brain size in primates vs. carnivores. In such cases, phylogenetic regression on the species level is not

appropriate to find the prevailing trend in mammals as a group, as the more speciose clade will determine the overall trend, or, as in our case of two clades of equal sample size, the opposing trends will cancel each other. Therefore, we also analyzed mammals on the suborder level, which gives appropriate weight also to suborders with only a few or single members. Lambda was zero in this sample, indicating that taking suborder means effectively corrected for phylogenetic dependence. At that level, we found a significantly positive correlation between allomaternal care (PC1) and brain size also in mammals as a whole (cf. Figure 2).

The inclusion of potentially confounding variables, on the other hand, had very limited effects on the correlations between help and brain size or fertility. Nevertheless, it was important to include a rough measure of gregariousness in order to exclude the possibility that the observed effects are rather due to a social lifestyle than due to energetic effects of allomaternal care. When we excluded these confounding variables form the analyses, none of our conclusions changed.

The second prediction, that direct forms of help were more effective than indirect forms, was also supported by our results, although the details of which behaviors clustered together varied according to lifestyle. Provisioning and carrying were highly correlated with brain size or fertility. Allonursing was too, to a slightly lesser extent, whereas babysitting, retrieval and huddling, or protection, have a much weaker effect if they are not coupled to the direct forms of help. Interestingly, the three species of rodents that exhibit provisioning (*Castor canadensis, Onychomys leucogaster*, and *Octodon degus*) are very distantly related to each other, but all three have considerably larger brains than their relatives, strongly supporting the idea that energy inputs allowed brains to increase in size. Grasshopper mice, *Onychomys,* are the only true carnivores among rodents (Egoscue 1960) and are renowned for being violently aggressive toward

conspecifics other than their mates (Ruffer 1968). Whereas male *Onychomys leucogaster* are reported to provision their offspring (Burt and Grossenheider 1976; Ruffer 1965), males of its smaller-brained sister species *Onychomys torridus* only huddle and groom (McCarty and Southwick 1977). These three contrasts are largely responsible for the positive correlation between brain size and provisioning in rodents, and further, more detailed studies of them or other, hitherto unknown species of rodents exhibiting provisioning would be needed to corroborate this result.

Artiodactyla, on the other hand, never provision their offspring, and our results suggest that protection and babysitting do not have enough of an energetic benefit to exert an effect on fertility or brain size in this group. However, elephants exhibit a considerable amount of allomaternal care (mainly by other adult females, Lee 1987), and they have relatively larger brains than hoofed mammals (cf. Figure 2), to which they may best be compared due to their lifestyle and diet, although they are not directly related.

For Carnivora, our findings are directly opposite to the pattern found by Gittleman (1994), in that singly breeding carnivore mothers have relatively smaller brains than species with some allomaternal care. Most noteworthy, brain size data are almost identical in the two studies, as the measurements of Gittleman still provide the most comprehensive and reliable database of carnivore brain sizes. Therefore, the discrepancy may be partly attributed to the new data on social behavior that has been published in the last 15 years, and partly to the doubling of sample size (N=101 vs. N=50 terrestrial carnivores).

Turning now to the predictions that concern the development stage at birth, we predicted that precocial species with allomaternal help show a shift of their development mode toward the altricial end of the spectrum, if this can be done without increasing the

predation risk of the now more altricial offspring (prediction 3). In primates, we did indeed find a pronounced shift toward altriciality in species that provide more help, especially within New World monkeys. In most ungulates and elephants, predation risk of insufficiently precocial neonates prevents a shift towards altriciality. This option is only available if offspring are efficiently protected and defended within a nest, as in some species of Suidae, which have both relatively altricial offspring and communal care (e.g. peccaries). However, due to the rarity of this adaptation it was not detected in our phylogenetic analyses. On the other hand, we found a shift towards more precocial offspring with increased protection by males in Artiodactyla, and in rodents with more provisioning. In these groups, help thus seems to allow for a (gradual) change in life history towards the production of more precocial offspring with better chances of survival to adulthood (prediction 4), but this result is in need of corroboration by comparing juvenile survival rates.

Load reduction of mothers by a shortening of the strenuous lactation period (see Supplementary Information for evidence that the relative energetic load during gestation is lower than during lactation), exists in primates, and as a trend also in carnivores. Rodents, on the other hand, show an increase in the duration of the lactation period with indirect forms of help such as huddling, retrieval and protection. Again, more help tends to increase a quality-over-quantity strategy of offspring production in rodents. We did not observe any consistent correlations between allomaternal care and lifespan, perhaps because our data on maximum lifespan are not sex-specific.

In primates, the results of our PCA suggests that allonursing (occurring in 17% of the species and explaining 16% of the variation in helping behaviors) is not additive to other helping behaviors (i.e. just another element of helping, as suggested by e.g. the classification scheme of Hrdy (2010)), but rather an independent dimension of

allomaternal care, which is probably more related to patterns of relatedness and tolerance among adult females. With respect to the correlation of help with brain size and fertility our results confirm earlier studies (Mitani and Watts 1997; Ross and MacLarnon 2000): Help mainly increases fertility, as the high energetic load of carrying the offspring and lactating at the same time is alleviated through cooperative care. However, this strategy is most pronounced in New World monkeys. Callitrichid primates regularly produce twins, and the father and other group members carry them shortly after birth for most of the time (Digby et al. 2007). Here, the increased fertility has an interesting consequence. During gestation, the mother has to bear the energetic load of production alone. This burden is partly reduced by shortening gestation length, and giving birth to more altricial offspring with relatively smaller brains at birth (DeSilva and Lesnik 2008, their Figure 6), even if their small adult brains are taken into account. But nevertheless, in species that evolved twinning the energetic load during gestation became so large (e.g. Nievergelt and Martin 1999) that relative brain size was reduced, even relative to ancestral values in the callithrichid lineage (Montgomery et al. 2010). On the other hand, we found that allonursing is positively correlated with brain size in primates. However, rather than a weak energetic effect this may also reflect a higher level of tolerance in those species that exhibit allonursing, which facilitates social learning from conspecifics other than the mother and may thus increase the effectiveness of transferring enhanced cognitive abilities.

In sum, we found support for an energetic effect of help on brain size: an additional influx of energy into the mother-offspring unit, as provided e.g. by help of the male or non-breeding group members, is significantly correlated with brain size, but not with fertility, in most taxa groups and for most factors of help. The one notable exception are the nonhuman primates, especially the Neotropical platyrrhines, where a

strong negative effect of cooperative care on brain size is paired with a strong positive effect on fertility and altriciality of the offspring.

Allomaternal care and human evolution

How do humans fit into this picture? We will argue that the help, especially the provisioning, received by human mothers partly explain our increased brain size relative to the ancestral state and that the finding for primates, of help producing higher reproductive rates and more altricial young, also holds in humans.

Humans are cooperative breeders: group members of both sexes and including both reproductive men and non-reproductive group members, such as post-reproductive kinswomen (cf. Hawkes et al. 1998) and older siblings, help mothers in the form of food provisioning, carrying, protecting and babysitting the infants (reviewed in Hrdy 2009). Indeed, among foragers mothers are provided with more food (about 3500kJ per day, Kaplan et al. 2000) during both gestation and lactation than they actually need to cover the maximum additional costs of gestation or lactation (Butte and King 2005; Sellen 2007). Provisioning the children with mashed or cooked food that is both easy to chew and digest begins even before weaning and provisioning with solid food continues for years afterwards (Bogin 1998).

At the same time, humans are “secondarily altricial” (Portmann 1962) in so far as their brains are relatively immature at birth. In modern humans the brain has attained only 28.0% of adult size at birth compared to 40.1% in chimpanzees (DeSilva and Lesnik 2006) and our neonates are somewhat more helpless than those of our closest relatives, the great apes (Schultz 1949). Nonetheless, thermoregulatory ability and a high metabolic rate are already achieved by a few hours after birth, as in precocial mammals, even if a reversion to hypoxic hypometabolism is still possible for a few days

after birth (Singer and Mühlfeld 2007). The prevalent explanation for this more altricial state of the human neonate is that the narrowing of the pelvic canal as a result of bipedality has at one point in our evolutionary history become limiting for neonate head size (the "obstetrical dilemma;" see Montagu 1961; Trevathan 1987; Washburn 1960)). However, there is considerable debate about the time of origin (cf. DeSilva 2011) and even the existence (S. Pfeiffer, pers. comm.) of such a constraint. We argue that the increased efficiency of postnatal allomaternal care provides an alternative explanation for the relatively altricial state of human neonates at birth, which simultaneously explains other peculiarities of human developmental timing such as early weaning and shortened interbirth intervals. However, current data on fossils do not allow us to determine when these changes did occur, as neither tooth eruption patterns nor dental attrition in infants (Aiello et al. 1991) are conclusive in this respect (e.g. Skinner and Wood 2006, Dean 2010). The most promising approach to detect the age at weaning in fossils seems to be to look for changes in the stable isotope composition of enamel (see Humphrey 2010, Eerkens et al. 2011).

Overall, humans not only deviate from the primate trend through extensive provisioning of infants with high-quality food, but also through the provisioning of mothers and weaned offspring. In this respect humans resemble Carnivora, where we found that provisioning of mothers yields an additional positive effect on brain size. Provisioning of mothers increases the upper limit of maternal energy expenditure during gestation and lactation, and therefore allows for indirectly shunting energy towards the offspring's brain development. Provisioning of weaned offspring is likely to allow for earlier weaning, in line with our finding of a negative correlation between help and age at weaning in primates (and a trend in carnivores). However, it would be necessary to obtain more detailed data on brain development in cooperatively breeding carnivores to

be able to see whether post-weaning provisioning can still affect brain growth, or whether it instead facilitates the survival of a large-brained offspring, which is most vulnerable due to the mismatch between the already fully grown brain and its relatively small body. However, these energetic effects need not be found on a proximate level, as a direct mechanism. Thus, both experimental and comparative studies will be needed to investigate these effects, and gain further insight into human brain and life history evolution.

We do not argue that the approximately three-fold increase in brain size since the origin of the genus *Homo* is due entirely to help. Recently, we listed potential factors that may have played a role in human brain size increase in the Pleistocene (Navarrete et al. 2011). Building on earlier ideas (Aiello and Key 2002; Aiello and Wells 2002; Leonard et al. 2003; Martin 1983, 1996), we showed which of these factors are supported by general relationships that are also found in other mammalian lineages, and argued that special pleading for humans is not needed. These factors include the stabilization of energy intake on a higher level through a change in diet and cognitive and physiological buffering of seasonality effects (van Woerden et al. 2010; van Woerden et al. 2012) as well as a reduction of energy spent on locomotion through abandonment of climbing and a more efficient bipedalism (Pontzer et al. 2010). The present study suggests that energy subsidies for mothers and infants play a major role in the stabilization of energy intake.

These various changes are related. Indeed, we have argued (Isler & van Schaik in review) that a change in lifestyle towards cooperative care could have been the first step towards encephalization, as the adaptation of cooperative breeding itself is clearly not dependent on high cognitive abilities (e.g. mole-rats, callitrichids, meerkats). However, because it was combined with an already ape-like cognition, cooperative

breeding in early *Homo* may have had unprecedented consequences. In our scenario, social tolerance increased, opportunities for social learning of ecological skills arose more frequently (van Schaik and Burkart 2011), and a skill-intensive niche, relying on tool-based processing of meat or marrow, was gradually occupied (or constructed, cf. Iriki 2008; Kaplan et al. 2000; Laland et al. 2000). Shared intentionality and frequent food sharing between adults (Jaeggi and van Schaik 2011) facilitated joint defense and thus exploitation of big game carcasses (e.g. Pobiner et al. 2008). Within a relatively short time, the innovation of cooperative hunting and perhaps cooking (cf. Carmody et al. 2011) spread among the cooperatively breeding early hominins, and the ensuing more stable supply of high quality food allowed for a further increase in both fertility and brain size. At one point, care for sick or injured group members also reduced adult mortality, which allowed humans to gradually evolve a longer lifespan (cf. the find of an old toothless individual in Dmanisi, 1.77 MA bp, Rightmire et al. 2006). Studies of birds found that cooperative breeding is more frequent in open habitats such as savanna (Rubenstein and Lovette 2007), and the first out-of-Africa event indicates that of early *Homo* must have had relatively high reproductive rates.

We conclude that brain size increase in the hominin lineage was only feasible after substantial energetic inputs due to helping, and particularly provisioning of pregnant mothers, had evolved, signaling the origin of cooperative breeding in our lineage. But in addition to that, the psychological characteristics of a cooperatively breeding primate, in combination with an already rather large hominoid brain, produced the rapid and unparalleled brain expansion of modern humans (cf. Burkart et al. 2009; Burkart and van Schaik 2010; van Schaik and Burkart 2010).

Tables

Table 1: Principal components analysis of helping behaviors in placental mammals

a) in placental mammals

Non-phylogenetic PCA					Rotated factor loadings					
					Comm. nesting		Provision		Carry	
	Label	Eigen-value	% Var. expl.	Allo-nursing	/ babysit / retrieval	Protect	Male	Others	Male	Others
PC1	Allocare	3.333	47.6	0.112	**0.675**	**0.720**	**0.840**	**0.801**	**0.726**	**0.672**
PC2	Allonursing	1.132	16.2	**0.858**	0.318	0.187	0.097	0.191	-0.362	-0.319

b) within large orders

Non-phylogenetic PCA							Rotated factor loadings				
						Comm. nesting		Provision		Carry	
Group		Label	Eigen-value	% Var. expl.	Allo-nursing	/ babysit / retrieval	Protect	Male	Others	Male	Others
Carnivora	PC1	Allocare	3.318	66.4	0.102	**0.827**	**0.952**	**0.899**	0.615		
	PC2	Allonursing	0.931	18.6	**0.964**	0.307	0.131	0.140	**0.633**		
Rodentia	PC1	Provision	2.175	43.5	-0.157	0.148	0.230	**0.953**	**0.955**		
	PC2	Allocare	1.462	29.2	**0.528**	**0.865**	**0.825**	0.099	0.013		
Primates	PC1	Allocare	3.868	55.3	0.034	**0.729**	**0.613**	**0.938**	**0.891**	**0.828**	**0.749**
	PC2	Allonursing	1.153	16.5	**0.888**	-0.236	-0.419	-0.015	0.158	-0.291	0.252
Artiodactyla	PC1	Allocare	1.511	50.4	**0.865**	**0.871**	-0.017				
	PC2	Protect	1.005	33.5	-0.109	0.076	**0.996**				

Table 2: Phylogenetic multivariate regression models (PGLS) of the components of help on brain size, A) in mammals (on the level of suborders), B) in mammals (species-level), and C) within large orders. Note that in C), the nature of help summarized by PC1 and PC2 differs for the various orders, see Table 1b. For help factors and covariates, the table lists p-values followed by the direction of the effect (+ or -). Lambda values are estimated by Maximum Likelihood, the number of asterisks indicates significant differences from 0 or 1 (***: significantly different from both 0 and 1, **: significantly different from 1, *: significantly different from 0).

Brain size					**Help factors from PCA**			**Covariates**			
	N	**lambda**	**adjR2**	**AICc**	**PC1**	**PC2**	**Grega-riousness**	**Diet**	**Activity**	**Substrate**	**Body mass**
A)											
Suborders	28	0**	0.973	39.7	**0.023+**	0.775+	0.873+	0.176-	0.800+	0.212+	<0.0001+
B)											
All mammals	445	0.978***	0.903	-123.1	0.397+	0.111+	0.497+	**0.002-**	0.788+	0.117+	<0.001+
C)											
Carnivora	101	0.953***	0.931	-53.9	**0.001+**	**0.025+**	0.104-	0.146-	0.548+	0.320+	<0.001+
Rodentia	113	0.915***	0.937	-58.9	**0.018+**	0.087+	0.739-	0.076-	0.878+	**0.026+**	<0.001+
Primates	98	0.989***	0.888	-79.5	**0.010-**	**0.037+**	0.251+	0.231-	0.746+	0.432-	<0.001+
Artiodactyla	66	0.995*	0.903	-15.9	0.185+	0.873-	0.088+	0.411+	0.395-		<0.001+

Table 3: Phylogenetic multivariate regression models (PGLS) of the components of help on fertility, A) in mammals (on the level of suborders), B) in mammals (species-level), and C) within large orders. Note that in C), the nature of help summarized by PC1 and PC2 differs for the various orders, see Table 1b. For lambda values, see legend of Table 2.

					Help factors from PCA		Covariates				
Fertility	**N**	**lambda**	**adjR2**	**AICc**	**PC1**	**PC2**	**Grega-riousness**	**Diet**	**Activity**	**Substrate**	**Body mass**
A)											
Suborders	28	0**	0.710	63.9	0.183-	**0.034+**	0.749-	0.679+	0.811+	0.331-	<0.001-
B)											
All mammals	406	0.913***	0.213	523.4	**0.013+**	0.282+	0.351-	0.211+	0.127+	0.285-	<0.001-
C)											
Carnivora	98	0.798***	0.179	134.8	0.779-	0.076+	0.923-	0.967+	0.522+	0.506+	<0.001-
Rodentia	99	0.889***	0.105	144.3	0.782-	0.732+	0.950-	0.484-	0.385+	0.522-	<0.001-
Primates	84	0.673**	0.602	88.5	**0.002+**	0.589-	0.080+	0.610-	0.867+	0.098-	<0.001-
Artiodactyla	60	0.895***	0.152	63.0	0.196+	0.381-	0.161-	0.278+	0.065+		<0.001-

Table 4: Phylogenetic multivariate regression models (PGLS) of the components of help on gestation length, lactation length, age at first reproduction (AFR) and maximum lifespan. Note that PC1 and PC2 differ according to the analysed group, see Table 1b. For lambda values, see legend of Table 2.

						Help factors from PCA			Covariates			
Life history												
Group	**LH trait**	**N**	**lambda**	**adjR2**	**AICc**	**PC1**	**PC2**	**Grega-riousness**	**Diet**	**Activity**	**Substrate**	**Body mass**
Suborders	gestation	28	0**	0.271	78.5	0.987-	0.390-	0.344-	**0.017-**	0.072-	0.099+	0.009+
	lactation	27	0	0.083	87.5	0.723-	0.437-	0.330-	0.081-	0.373-	0.141+	0.052+
	AFR	28	1	0.366	82.3	0.105-	0.861-	0.143-	**0.016-**	0.585-	0.042+	0.008+
	max Lifespan	27	0	0.204	69.3	0.845-	0.505-	0.161-	0.087-	0.155-	0.123+	0.016+
All mammals	gestation	416	0.995*	0.250	-150.4	0.560+	0.692+	0.384+	**0.044-**	0.631+	0.680+	<0.001+
	lactation	418	0.605***	0.088	1289.1	0.432-	0.074+	0.903+	0.090-	0.309+	0.186-	<0.0001+
	AFR	427	0.693***	0.179	840.1	0.338+	0.673-	0.511-	0.441-	0.321+	0.138+	<0.0001+
	max Lifespan	394	0.230***	0.171	972.7	**0.040+**	0.143+	0.827+	**0.046-**	0.079-	**0.0001+**	<0.0001+
Carnivora	gestation	97	0.971*	0.170	-26.3	0.588-	0.971+	0.268+	0.224-	0.141+	0.932+	<0.0001+
	lactation	90	0.863***	0.386	94.6	0.083-	0.147-	**0.041+**	0.537+	0.601+	0.796+	<0.0001+
	AFR	91	0.719***	0.437	88.8	0.926-	0.875+	0.477+	0.362+	0.605+	0.905-	<0.0001+
	max Lifespan	93	1*	0.268	-0.32	0.418+	0.395+	0.636+	**0.009-**	0.105+	0.051+	<0.0001+
Rodentia	gestation	105	1*	0.247	-51.5	**0.005+**	0.094+	0.408-	0.987+	0.323-	0.326+	<0.0001+
	lactation	103	0.840***	0.239	29.9	0.460+	**0.003+**	0.056-	0.259-	**0.036+**	**0.040+**	<0.0001+
	AFR	103	0.675***	0.304	173	0.323+	0.572-	0.695-	0.840-	0.515+	0.286+	<0.0001+
	max Lifespan	94	0.784***	0.236	107.4	0.084+	0.308+	0.595+	0.609-	0.046-	0.072+	<0.0001+
Primates	gestation	84	0.982***	0.272	-112.6	**0.037-**	0.642-	0.928+	0.411+	0.138+	0.915-	0.001+
	lactation	85	0.794***	0.634	82.8	**0.017-**	0.072+	0.611-	0.293+	0.610+	0.197+	<0.0001+
	AFR	84	1*	0.076	52	0.462-	0.549+	0.984+	0.641+	0.571+	0.763+	0.007+
	max Lifespan	87	0.821**	0.344	-23.6	0.803-	**0.034+**	0.862-	0.594-	0.727-	0.344+	<0.0001+
Artiodactyla	gestation	65	1*	0.410	-55.3	0.890+	**0.0003+**	0.844+	0.327-	0.588+		<0.0001+
	lactation	52	0.573**	0.506	45.6	0.231-	0.484+	0.810+	0.255+	0.231+		<0.0001+
	AFR	60	0**	0.597	57.9	0.598-	0.707+	**0.010+**	0.053-	0.909+		<0.0001+
	max Lifespan	64	0.729	0.386	-12.6	0.112+	0.774+	0.161+	0.545-	0.282-		<0.0001+

Table 5: Phylogenetic multivariate regression models (PGLS) of the components of help and provisioning of mothers on brain size, fertility, gestation length, lactation length, age at first reproduction (AFR) and maximum lifespan, in Carnivora. For lambda values, see legend of Table 2.

				p-values of help factors				p-values of covariates		
Carnivora	**N**	**lambda**	**adjR2**	**PC1**	**PC2**	**Provision of mothers**	**Grega-rious-ness**	**Diet**	**Activity**	**Body mass**
Brain size	27	0**	0.978	0.087+	0.363+	**0.022+**	0.522-	0.112-	0.592+	<0.0001+
Fertility	27	0.730**	0.194	0.840-	0.086+	0.765+	0.413-	0.547+	0.097+	0.575-
Gestation	26	1	0.045	0.940-	0.186-	0.315-	0.067+	0.647-	0.733-	0.226+
Lactation	25	0.885*	0.465	0.053-	**0.016-**	0.751-	**0.007+**	0.785-	0.181-	0.065+
AFR	27	0.976*	0.596	0.504+	0.313+	0.399+	0.871+	**0.025+**	0.101-	0.013+
Max. lifespan	27	1*	0.305	0.336+	0.606+	0.366-	0.331+	0.079-	0.239+	0.019+
Control: same sample without the variable “provisioning of mothers”										
Brain size	27	0**	0.972	**0.0005+**	0.156+		0.225-	0.034-	0.223+	<0.0001+

Figure legends

Figure 1: Prevalence of helping behaviors within mammalian groups (N=445 species). Numbers indicate number of species known to show the behavior.

Figure 2: Correlations between brain size and factors of allomaternal help in mammals at the level of suborders. Factors of help are the first two rotated components of the non-phylogenetic principal components analyses (cf. Table 1a). The mean residuals of brain size (and mean help factors, respectively) are the mean residuals for all species in the suborder, derived from multiple least-squares models including body mass, diet, substrate use, and activity. P-values (p_{raw}) of least-squares regressions between these residuals are shown, with the direction of the effect shown in parentheses. Details of phylogenetic models are shown in Table 2a, and the p-values (p_{PGLS}) are noted on the graphs.

Figure 3: Correlations between brain size and factors of allomaternal help in large mammalian orders. A) fissiped Carnivora, B) Rodentia, C) Primates, and D) Artiodactyla. Factors of help are the first two rotated components of the non-phylogenetic principal components analyses (cf. Table 1b). For Rodentia, the first factor of non-phylogenetic ("provision") and the second factor of phylogenetic PCA ("protect", cf. Appendix Table 2) are shown (see text for an explanation). The mean residuals of brain size (and help factors, respectively) are the mean residuals for all species derived from multiple least-squares models including body mass, diet, substrate use, and activity. P-values (p_{raw}) of least-squares regressions between these residuals are shown, and the direction of the effect is shown in brackets. Details of phylogenetic models are shown in Table 2c, and the p-values (p_{PGLS}) are noted on the graphs.

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